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THE PHYLOGENY OF THE TERMITES.

WILLIAM MORTON WHEELER.

Among the changes that have been suggested within recent years in the classification of the larger groups of insects, none are more important than those affecting certain groups isolated by Burmeister ('39) and Brauer ('85) under the designation Corrodentia from the miscellaneous complex variously known to the older entomologists as Orthoptera, Neuroptera and Pseudoneuroptera. For Burmeister the Corrodentia embraced the Termitidæ ("white ants"), the Embiidæ and the Psocidæ ("book-lice"). Brauer included under the Corrodentia the Termitidæ, the Psocidæ and the Mallophaga ("bird-lice"), but assigned the Embiidæ to the Orthoptera with a query. More recently some authors have been inclined to combine the classifications of Burmeister and Brauer. Enderlein ('03), for example, divides the order Corrodentia into three suborders, one comprising only the Psocidæ and called by him Copegnatha, another comprising the Mallophaga, and a third (Isoptera), sharply separated from the two others and comprising the Termitidæ and the Embiidæ.

Börner ('04) has raised Enderlein's suborder Isoptera to ordinal rank and thus removed the termites and Embiids from the order Corrodentia, in which he leaves only the Psocidæ and the Mallophaga.

Handlirsch, in two valuable and suggestive papers on the classification of insects ('03 and '04), maintains that the Corrodentia (in the sense of Enderlein) must be resolved into four different orders: the Isoptera, in Comstock's sense ('99, pp. 96–97),[1] and including the termites only, the Psocidæ, to which Handlirsch limits the term Corrodentia, the Mallophaga (Nitsch) and the Embiaria (Handlirsch). Far from regarding the Embiids as related to the termites, he places these groups in different subclasses (Blattæformia and Embioidea). Thus the old

[1] I infer from Hagen's monograph of the termites ('58), that the term Isoptera goes back to Brullé and was by him used in the sense of Termitidæ. If this is true the term and conception should not be attributed to Comstock.

group Corrodentia has undergone a complete taxonomic disintegration, and it would probably be best to abandon the term altogether and not limit it with Handlirsch to the Psocidæ.

Shipley ('04), in a paper devoted to the emendation of the names of the insect orders, follows Sharp, who seems to agree with Handlirsch in recognizing four independent orders: Isoptera (Termitidæ), Embioptera (Embiidæ), Psocoptera (Psocidæ) and Lipoptera (Mallophaga). Three of these four ordinal names have been coined by Shipley for the sake of making all the insect orders end in *ptera*, after the well-known classical models. Both Handlirsch and Borner ('04) repudiate this attempt of Shipley, the former on the grounds of priority, the latter because some of these names, like Psocoptera and Embioptera are by no means homogeneous in their formation with the classic examples Lepidoptera, Coleoptera, Neuroptera, etc. It seems to me that if the law of priority in nomenclature is to mean anything, it must be applied to the names of the larger groups as rigorously as to the names of genera and species.

Concerning the termites, with which I am more concerned in this paper, Handlirsch ('04, p. 738) makes the following statement: ". . . they have been regarded as having a very primitive organization, and the circumstance that many paleozoic and mesozoic forms have been (erroneously) claimed to be termites, seemed to support this view. Among other characters the homonomy of the wings has been interpreted as primitive. A study of these organs, however, shows that they are highly specialized and that the homonomy has come about through atrophy of the anal border of the fore and hind wing. The termite wing is a Blattid wing with strongly reduced anal area, so that the homonomy is a secondary condition. Quite as highly modified are the termites in respect to their polymorphism, the formation of societies, the reduction of the cerci, the multiplication and lengthening of the ovarioles, the reduction in the number of the Malpighian vessels, etc. The feebler concentration of the thoracic segments seems to have accompanied the specialization of the wings or rather the decrease in their function, and is, at all events, to be regarded as no more primitive than the similar condition in the fleas. It is quite as impossible to

derive the termites from the Embiidæ as the Embiids from the termites. The wings of the Embiids are specialized in an entirely different direction, the legs are more highly developed, as are also the abdominal appendages, the ocelli have disappeared, etc. With respect to their entire organization the termites may be derived without difficulty from the Blattids, which agree with them also in the position of the legs and in having large coxæ. Interesting is the existence of termite larvæ with prothoracic dilatations, which have no particular function and ultimately disappear."

In this paragraph Handlirsch clearly formulates a view which seems to have been gaining ground ever since Hagen, nearly half a century ago ('58, p. 31) insisted on the close affinity of the Termitidæ with the Blattidæ, or cockroaches.

At this point the subject has been taken up in an interesting paper by Desneux ('04), who has actually found in a North Australian termite (*Mastotermes darwiniensis* Froggatt) a form, which, though a true termite, is nevertheless structurally transitional between the Blattidæ and the other termites. This form, of which only the imago is known, is regarded by Desneux as representing a new subfamily (Mastotermitinæ) and leads him to propose the following arrangement of the Isoptera, or Termitidæ :

Isoptera, or Termitidæ
- Termitinæ
  - Termitini (*Termes*).
  - Rhinotermitini (*Rhinotermes* + *Arrhinotermes*).
- Calotermitinæ
  - Calotermitini
    - Calotermes.
    - *Termopsis*.
  - Hodotermitini
    - *Hodotermes* + *Podotermes* + *Stolotermes*.
- Mastotermitinæ
  - *Mastotermes*.

The blattoid characters of Mastotermes, as determined by Desneux, are the following : The wings have the typical blattoid neuration, both pairs have a distinct anal area, small and bounded by an arched groove in the fore wing, but in the hind wing highly developed and folded during repose. In the anterior wing the basal corneous portion is considerable. The neuration

of the hind wing is very different from that of the fore wing, and the anal lobe is clearly marked off by a deep notch. The head is without a fontanelle, the antennæ are long and 30-jointed, the labrum does not project, the prothorax is large, larger, in fact, than the head, the tibiæ have a row of spines along their sides and four spines at the apex. The tarsi are 5-jointed and furnished with a small pulvillus.

Desneux's study of Mastotermes thus supplies the keystone to a taxonomic arch which students of the lower insects have been building for some time past. The structure is, however, still incomplete, since only the facts of comparative anatomy seem to have been consulted, and due regard for the facts of paleontology, geographical distribution, embryology and ethology must be had before we can accept the derivation of the Termitidæ from the Blattidæ as established beyond contradiction. As Handlirsch has studied fossil insects extensively, it is probable that he has at least found nothing in paleontology to contradict his theory. In regard to geographical distribution there is no difficulty, but instead a singular resemblance between the two groups of insects in question, inasmuch as both of them are cosmopolitan and, with the exception of a very few species, confined to tropical and subtropical countries. In other words, countries which are most favorable to the development of Blattidæ also have a rich termite fauna. But how stands it with the embryology and ethology of the Blattidæ and Termitidæ? I believe that the views of Handlirsch and Desneux are not without some support from these sources also, as I shall attempt to show in the following paragraphs.

A number of investigators have studied the development of various Orthoptera, including the Blattidæ, and Knower ('00) has furnished us with a valuable paper on the embryology of a termite (*Eutermes*). In comparing the development of these insects with one another we are struck with the remarkable similarity between the termite and the Orthoptera, especially certain Saltatoria (Acridiidæ and Gryllidæ). This resemblance, which was recognized by Knower, is seen in the simple nature of the chorion, the absence of a vitelline membrane, the structure and consistency of the yolk, the great volume of the yolk as com-

pared with that of the incipient germ-band, the position of the latter on the posterior ventral surface of the egg, the pronounced anatreptic and katatreptic movements of the embryo, etc. Comparison of the termite with the Blattid shows great similarity in the structure of the micropyles, but, as I have pointed out ('89, '93), the blastokinetic, or embryonic movements in the latter insect are very feeble, not sufficient, in fact, to carry the embryo from the anterior to the posterior surface of the yolk. This slight movement I interpreted as a vestige of the more pronounced blastokinesis of the Saltatoria. If this view is correct, we must suppose the Termitidæ to have retained in the more pronounced movements of the germ-band somewhat more primitive orthopteroid conditions than the Gressoria (Blattidæ and Mantidæ). This is, of course, not necessarily fatal to a derivation of the termites from the Blattidæ, since a modification of the embryonic development in the direction of a partial suppression of blastokinesis may have supervened within the Blattid group after the Termitidæ had diverged from the more primitive family stock.[1]

At first blush there would seem to be no ethological relationship between the Blattidæ and the Termitidæ. The former are regarded as omnivorous insects without a social organization whereas the latter have a specialized diet of cellulose and present a social organization only equalled or surpassed in complexity by that of the ants, certain wasps and bees. Somewhat closer

[1] Knower seems to have misunderstood my position in regard to the superficial and immersed germ-bands of insects. At any rate his long discussion of this and kindred matters tends only to befog the whole subject. I expressly maintained ('93, p. 68) that the stationary, superficial germ-band is primitive in the Arthropoda in general, and probably also in the insects in particular, but that in the latter class blastokinesis, with or without immersion, early established itself since it is found in many primitive orders. Later these movements were abolished (the Blattidæ, *e. g.*, show them very feebly), so that the higher insects (Coleoptera, Hymenoptera, Diptera, etc.) have secondarily returned to the primitive type of an almost stationary, superficial germ-band. I believe the chief stress in these considerations is to be laid on the movements of the embryo and not on the more incidental superficiality or immersion of the embryo. Whether embryos like those in Knower's stages *M* and *N* (Pl. 33) are to be regarded as superficial or immersed is open to serious doubt. A form like the locustid *Xiphidium* is immersed during anatrepsis, but superficial during katatrepsis. In passing I may express my inability to conceive why Knower courts confusion by inverting all the figures of his termite embryos.

study, however, shows, unmistakable ethological similarities between the two families. Both are strongly heliophobic, or dark-loving (negatively heliotactic) animals and hence also positively contact-loving or thigmotactic. Our wild cockroaches, like the termites live in dead or decomposing wood or in the soil. Furthermore, it can be shown that there are adumbrations of social life among the Blattidæ. Our domestic species are somewhat gregarious in their adolescent and adult stages. Then, too, the mother cockroach deposits her eggs in a peculiar oötheca which she carries about in a kind of brood chamber formed by an infolding of the terminal segments of the abdomen. The oötheca is, however, deposited before the young hatch. Entomological treatises repeat the statement that the female "croton bug" (*Phyllodromia germanica*) assists the young in escaping from the oötheca. This observation is traceable to Hummel ('29) who recorded it in a work which has become rather rare. The pertinent passage may, however, be found quoted in full in the works of Audouin and Brullé ('35, pp. 36, 37) and Serville ('39, pp. 59, 60). The fact that in some of our species of Blattidæ the young can escape from the oötheca without maternal assistance, casts doubt on these old observations. The female in these species exhibits only the first rudiments of a social instinct in the care of the young till they are nearly ready to hatch.[1]

A further extension of maternal care is seen in the beautiful green South American cockroach, *Panchlora viridis*, which is sometimes imported alive into stores and houses in New York and Brooklyn. Riley, in three short papers ('90, '91*a*, '91*b*), claimed that this insect is viviparous, but a moment's examination of the very facts he has recorded, shows that it cannot even be regarded as ovoviviparous. In his third paper ('91*b*) he figures the semi-circular egg-mass of the insect with two rows of embryos arranged with their ventral surfaces face to face, just as others and myself have shown them to be arranged in the oötheca of *Phyllodromia* and *Periplaneta*. Moreover, a delicate

[1] That the maternal instincts of the "croton bug" are highly variable is proved by an observation communicated to me by Mr. Wm. Beutenmüller while these pages are going through the press. He found one of these insects surrounded by her young and still retaining in her oöthecal chamber the empty oötheca from which they had just escaped.

membrane, which Riley himself interprets as a vestigial oöthecal envelope, encloses at least the posterior half of the eggs. Now this egg-mass, which is obviously only a slightly modified oötheca, is, according to Riley's statement, enclosed, not in the reproductive organs proper or body cavity of the mother insect, but in the oöthecal chamber. But this chamber, which also embraces at least one end of the oötheca in other Blattidæ, is morphologically *outside* of the body. Hence there can be no viviparity or even ovoviviparity in this case. *Panchlora* simply retains the oötheca completely within the oöthecal chamber till the young are ready to hatch.[1] This Blattid therefore represents a further stage in the care of the brood than is to be found in our domestic cockroaches.[2]

A more advanced, though still very crude, stage of social organization seems to be represented in certain Blattidæ like the singular North American *Dasyposoma* (*Cryptocercus*) *punctulata* Scudder ('62, pp. 419–421). This insect, which has been recorded from Virginia, North Carolina, Pennsylvania and New York, appears to be a very primitive form. v. Wattenwyl ('93), Scudder ('97, pp. 13, 15) and de Saussure ('95*b*) regard it as belonging to the subfamily Panesthinæ, a group comprising a number of Australian and Oriental species.[3] Comparison of a fine series of this insect collected by Mr. Wm. Beutenmüller in the mountains of North Carolina, with a series of the Australian *Panesthia cribrata* Saussure in the Edwards Collection of the American Museum of Natural History shows many striking resemblances in shape, color, punctulation, etc. Both sexes of

[1] This interpretation of Riley's work is confirmed by an examination of two dried female specimens of *Panchlora viridis* in the collections of the American Museum of Natural History. Each showed a shrivelled oötheca in the oöthecal chamber. On dissecting one of the specimens I found the oötheca to be of large size and bent in the form of a *C*, with its two ends almost meeting. It contained seventy-two embryos arranged in two series as in the common cockroaches.

[2] Among primitive insects the Forficulidæ, or earwigs, have long been known to care for their eggs, collecting them when dispersed and, according to some observers, even carrying them to places of more favorable temperature and moisture. Similar habits must be very ancient among the air-breathing arthropods as we find them well developed in certain Myriopods (*Geophilus*), which not only brood over their eggs but guard their young after hatching.

[3] De Saussure und Zehntner ('95*a*) however, include *Cryptocercus* in another primitive subfamily, the Perisphæriinæ.

the American species, however, are apterous. Mr. Beutenmüller has given me some notes on the habits of this insect. He found it living in colonies of fifty or more individuals, old and young together, burrowing in stumps, most frequently of oak trees, that had nearly or quite reached the red stage of ligneous decay. The burrows were sharply defined and close together and reminded him of the burrows of the beetle *Passalus cornutus*. Here we have a resemblance to the termites not only in the rude social life but also in the wood-boring habit.

Further observations on *Dasyposoma* and other Blattidæ are much needed and may perhaps enable us completely to bridge the gap that separates the rudimental social instincts of such insects from the complex social instincts of the Termitidæ. The recent revival in the study of termites certainly calls for a renewed interest in the habits of the much neglected Blattidæ.

BIBLIOGRAPHY.

Audouin, V. and A. Brullé.

'35. Histoire Naturelle des Insectes. Tome 9, Orthoptères et Hémiptères, Paris, 1835.

Börner, C.

'04. Zur Systematik der Hexapoden. Zool. Anzeig., 27, Bd. No. 16–17, 1904, pp. 511–533, 4 figs.

Brauer, F.

'85. Systematisch-zoologische Studien. Sitz. B. kais. Akad. Wiss. Wien. Math. naturwiss. Cl., 91. Bd., 1885, pp. 237–413, 1 Taf.

Burmeister, H.

'39. Handbuch der Entomologie. 2. Bd., Berlin, 1839.

Comstock, J. H. and A. B.

'99. A Manual for the Study of Insects, Third ed., 1899.

Desneux, J.

'04. A Propos de la Phylogénie des Termitides. Ann. Soc. Ent. Belg., T. 48, 1904, pp. 278–286, 3 figs.

Enderlein, G.

'03. Ueber die Morphologie, Gruppierung und systematische Stellung der Corrodentien. Zool. Anzieg., 26. Bd., nos, 698–699, 1903, pp. 423–437, 4 figs.

Hagen, H.

'58. Monographie der Termiten. Linnæa Entomologica, 12. Bd., 1858, pp. 1–342, 3 Tab.

Handlirsch, A.

'03. Zur Phylogenie der Hexapoden. Sitz-B. kais. Akad. Wiss. Wien. 92. Bd., 1903.

Handlirsch, A.

'04. Zur Systematik der Hexapoden. Zool. Anzeig., 27. Bd., No. 23–24, 1904, pp. 733–759.

Knower, H. McE.

'00. The Embryology of a Termite, Eutermes (Rippertii?) Journ. Morph., Vol. 16, No. 3, 1900, pp. 505–568, pl. 29–32.

Riley, C. V.

'90. A Viviparous Cockroach. Ent. Soc. Wash., Vol. 2, No. 1, 1890, pp. 129, 130.

Riley, C. V.

'91a. A Viviparous Cockroach. Insect Life, Vol. 3, 1891, pp. 443, 444.

Riley, C. V.

'91b. Further Notes on Panchlora. Insect Life, Vol. 4, 1891, pp. 119, 120.

de Saussure, H. and Léo Zehntner.

'95a. Revision de la Tribu des Perisphæriens. Insectes Orthoptères de la famille des Blattides, Rev. Suisse Zool., T. 3, fasc. 1, 1895, pp. 1–59, 1 tab.

de Saussure, H.

'95b. Revision de la Tribu des Panesthiens et de celle des Épilampriens. Insectes Orthoptères de la famille de Blattides. Rev. Suisse Zool., T. 3, fasc. 2, 1895, pp. 299–264, tab. 9.

Scudder, S. H.

'62. Materials for a Monograph of the North American Orthoptera, including a Catalogue of the Known New England Species. Bost. Journ. Nat. Hist. Vol. 7, No. 3, 1862, pp. 409–480.

Scudder, S. H.

'97. Guide to the Genera and Classification of the North American Orthoptera found North of Mexico. Cambridge, 1897.

Serville, A.

'39. Histoire Naturelle des Insectes. Orthoptères. Suites à Buffon. Paris, 1839.

Shipley, A. E.

'04. The Orders of Insects. Zool. Anzeig., 27. Bd., No. 7–8, 1904, pp. 259–262.

von Wattenwyl, Brunner.

'93. Revision du Système des Orthoptères. Ann. del Mus. Civico di Genova, ser. 2, T. 13, 1893.

Wheeler, W. M.

'89. The Embryology of Blatta germanica and Doryphora decemlineata. Journ. Morph., Vol. 3, No. 2, Sept., 1889, pp. 291–386, pl. 15–21.

Wheeler, W. M.

'93. A Contribution to Insect Embryology. Journ. Morph., Vol. 8, No. 1, 1893, pp. 1–160, pl. 1–6.